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A REVIEW OF THE EASTERN NORTH
AMERICAN SQUALODONTIDAE
(MAMMALIA: CETACEA)

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A Review of the Eastern North American Squalodontidae (Mammalia: Cetacea)

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He saw that in this dusty and fathomless matter of learning the true name of every place, thing, and being, the power he wanted lay like a jewel at the bottom of a dry well. For magic consists in this, the true naming of a thing. So Kurremkarmerruk had said to them, once... "Many a mage of great power," he had said, "has spent his whole life to find out the name of one single thing—one single lost or hidden name. And still the lists are not finished. Nor will they be, till world's end.

...Ursula K. LeGuin, *A Wizard of Earthsea*

ABSTRACT

Previous listings of species of the cetacean family Squalodontidae give the appearance of a diverse, well-represented group, but nearly all of the named specimens from North America are based on extremely poor material or were improperly proposed. This paper reviews the descriptions of these species and their type specimens to determine their validity.

Of 16 species from North America examined in the study, only two are members the family Squalodontidae, and only one, *Squalodon calvertensis* Kellogg, 1923, is based on material sufficient for reliable identification. An additional unnamed squalodont species is identified. Thus the diversity of Miocene Squalodontidae in North America was much lower than has been indicated in the literature.

INTRODUCTION

The Squalodontidae are a family of extinct odontocete cetaceans, found principally in Europe and eastern North America in late Oligocene to middle Miocene age strata. Two factors have led to some confusion about the status of this family. First, fossil remains of squalodonts are relatively rare, and often are very fragmentary; there is not even a complete composite skeleton for any species of squalodontid. Second, squalodonts are rather primitive compared to their Miocene contemporaries. These factors have led to the family becoming a "catch-all" for almost any poorly preserved primitive whale of Miocene age. Some species and specimens have been questionably referred to the Squalodontidae, resulting in a confused nomenclature that is in need of clarification.

A number of authors have reviewed squalodontid nomenclature, most significantly Kellogg (1923), Rothausen (1968), Ray (1976), Muizon (1991, 1994), and Fordyce (1981). This paper is an examination of the North American specimens that have been referred to Squalodontidae or at one time or another been considered to be squalodontids. By 1926 there were 16 type specimens from deposits in eastern North America referred to the Squalodontidae.

Muizon (1991, 1994) and Fordyce (1981, 1994) have attempted to restrict the definition of the Squalodontidae. Based in part on their work, the following characters are suggested as Squalodontidae apomorphies: 1) a spongy posterior process of the tympanic bulla; 2) reduction of the lateral lamina of the pterygoid hamulus (as in Muizon, 1991, 1994); 3) an upturned rostrum and mandible, 4) incisors that are nearly circular in cross section throughout their length, and straight with serrate edges; 5) an upper I1 alveolus that lies directly dorsal to the upper I2; 6) teeth that are serrate with heavily ornamented enamel from the base to the apex, increasing on posterior teeth, with ornamentation consisting of short ridges (the *cristae rugosae* of Rothausen, 1968), extending toward the apex, each ridge extending approximately 5 mm or less; and 7) cervical

vascular sinuses on Ce4-Ce6 only. Another important feature of the Squalodontidae, though not an apomorphy, is the degree of telescoping. In squalodontids the posterior ends of the maxillae are nearly in contact with the supraoccipital, and the parietals are almost (or completely) covered in dorsal view. Genus-level and species-level characters are not considered in this paper, and will be addressed in a future study.

Institutional abbreviations: AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences of Philadelphia; MCZ = Museum of Comparative Zoology, Harvard University; USNM = National Museum of Natural History, Smithsonian Institution

SAUROCETUS GIBBESII Agassiz, 1848

Saurocetus gibbesii Agassiz, 1848 is based on a single cheek tooth, possibly from late Oligocene deposits of South Carolina (MCZ 8760; Figure 1). The tooth has very simple ornamentation with no *cristae rugosae*, excluding it from the Squalodontidae. My examination of undescribed specimens in the Charleston Museum suggests that it has affinities with “Genus Y” of Whitmore and Sanders (1977), from late Oligocene beds near Charleston. “Genus Y” has less complete telescoping than do the squalodontids, and the taxon apparently represents a more primitive cetacean. Until more complete material is discovered, *Saurocetus gibbesii* should be placed in *Odontoceti incertae sedis*.

AGOROPHIUS PYGMAEUS (Müller), 1849

Agorophius pygmaeus (Müller), 1849 is based on a skull and tooth from late Oligocene deposits of South Carolina, which were originally figured by Toumey (1847) as “a cranium of the *Zeuglodon*.” It was transferred to the genus *Squalodon* by Leidy (1869), but Cope (1895) erected the genus *Agorophius* for this species, and the family

Agorophiidae was established by Abel (1914). Whitmore and Sanders (1977) classified *Agorophius* as Odontoceti *incertae sedis*. The holotype



Figure 1. *Saurocetus gibbesi*. Agassiz, 1848. Holotype, MCZ 8760, tooth. Scale = 10 mm.

skull of *A. pygmaeus* has been lost, but Fordyce (1981) redescribed the species based on figures of the holotype, and resurrected the Agorophiidae. *Agorophius* is much more primitive than any squalodontid, with less pronounced telescoping of the cranium and a prominent intertemporal constriction. The teeth have much less ornamentation than is observed in the squalodontids (Fordyce, 1981). Fordyce (1981) excluded the Agorophiidae from the Squalontoidea (the superfamily which includes the Squalodontidae) because of its lack of any synapomorphies shared with the squalodontids.

COLOPHONODON HOLMESII Leidy, 1853b

Colophonodon holmesii Leidy, 1853b was based on a tooth from South Carolina. Cope (1867b) transferred this species to *Squalodon*, and Kellogg (1923) noted that the species is represented by one nearly complete tooth and fragments of five others. Leidy (1869) suggested that the teeth may be related to *Agorophius*, but Kellogg (1923) stated that

"The remains are altogether too incomplete to propose any definite allocation in the light of or present knowledge of the fauna of these phosphate deposits". This statement is academic now, as the holotype specimen has apparently been lost. Kellogg (1923) thought that the holotype material was "possibly in the Academy of Natural Sciences at Philadelphia" but Gillette (1975) and Spamer et al. (1995) did not list these specimens among the types housed in the Academy, and I have been unable to locate them.

MACROPHOCA ATLANTICA Leidy, 1856a

Macrophoca atlantica Leidy, 1856a was based on three teeth (ANSP 11217, 11218, and 11219) from Cumberland County, New Jersey (Figure 2). These teeth are not definitely from the same individula, and as Leidy did not designate one tooth as the type, ANSP 11218 (the tooth with 2 complete roots) is herein designated as the lectotype, with ANSP 11217 and ANSP 11219 as paralectotypes.

Cope (1867a) listed *Squalodon atlanticus* among remains from the Thomas collection, discovered in Charles County, Maryland, citing Leidy as the author of this species: "... a fragment of the muzzle, including the proximal portions of the maxillary bones, with molars, and the canine teeth of the *Squalodon Atlanticus* (Leidy)." Cope (1867b) later clarified this referral with a more detailed description:

Squalodon Atlanticus Leidy MS. *Macrophoca atlantica*
Leidy, Proceed. Acad. 1856, 220.

Remains of three individuals of this species
before me indicate considerable variety in the forms of
the two rooted molar teeth.

The individual from which Leidy determined the
species is represented by only three true molars....

The second individual is represented in the
Thomas collection by the proximal portions of the

maxillary bones of both sides, and seven molar teeth in place....

The third individual is represented by one true molar, and two caniniform premolars....

No. 1 was discovered in the miocene of New Jersey; the others were in the Thomas collection.

The "second individual" described by Cope are ANSP 11220 and 11221 (Figure 3a-d). This is also the specimen mentioned by Cope (1867a) in his earlier reference to *S. atlanticus*. However, there has been some uncertainty concerning the status of ANSP 11221. Case (1904) figured a maxilla fragment as *S. atlanticus* (Figure 3e), with the following caption:

Figs. 1-3 *Squalodon atlanticus* Leidy

1. Portion of the right side of a jaw containing three teeth. Shiloh, N. J. Acad. Nat. Sci., Phila.

This specimen is clearly ANSP 11221, the maxilla fragment from Charles County, Maryland described by Cope (1867a, 1867b) (compare Figures 3c and 3e). The caption reference to Shiloh, New Jersey was in error. As Leidy's original specimens were from New Jersey this has apparently led some workers to believe that ANSP 11221 was the type specimen. For instance, Spamer et al. (1995) cited Case (1904) with the following note: "The holotype teeth [of *Squalodon atlanticus*] in jaw fragment are illustrated in [Plate 10] fig.1."

Allen (1916) referred *S. atlanticus* to *Basilosaurus* but Kellogg (1923) correctly noted that there was no basis for this action, and he returned the species to *Squalodon*. I have examined both Leidy's holotype teeth and Cope's referred specimens. They are typical of squalodont teeth as described in character 6 above, and they can thus be considered as belonging in the Squalodontidae. As mentioned by Kellogg

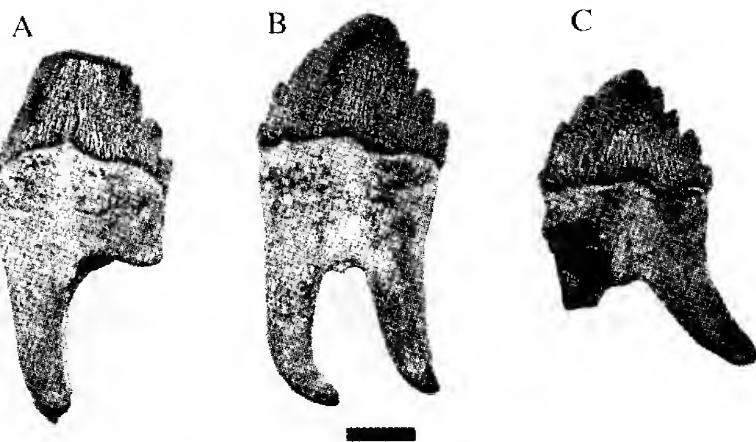


Figure 2. *Squalodon atlanticus*. A. ANSP 11217 (paralectotype), B. ANSP 11218 (lectotype), C. ANSP 11219 (paralectotype), teeth. Scale = 10 mm.

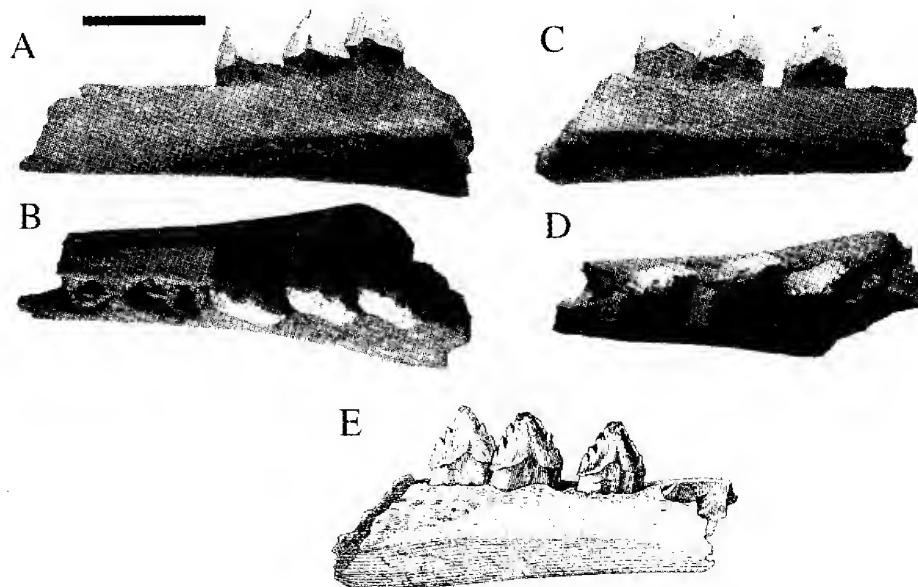


Figure 3. *Squalodon* sp., ANSP 11220, maxillary fragment, A. lateral, B. ventral. ANSP 11221, maxillary fragment, C. lateral, D. ventral. Scale = 50 mm. E. Case (1904), Plate 10, Figure 4. Compare Figure 3c and Figure 3e.

(1923), *S. atlanticus* is quite similar to *S. calvertensis*. Because of their extreme variability in cetaceans, teeth are of limited value in identifying specimens below the family level. Thus *S. atlanticus* should be placed in Squalodontidae *incertae sedis*. Cope's mandible fragments (ANSP 11220 and 11221) should therefore not be referred to *S. atlanticus*, but are instead considered *Squalodon* sp. until their affinities can be determined.

SQUALODON MENTO Cope, 1867a

Squalodon mento Cope, 1867a was based on four teeth from the Miocene of Charles County, Maryland. According to Cope (1867a) they "were between two and three times as large as those belonging to *Squalodon wymani* (*Phoca* of Leidy)".

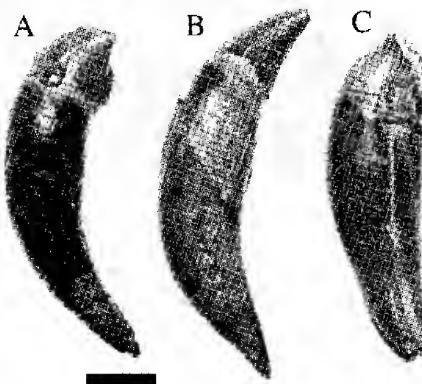


Figure 4. *Squalodon mento* Cope, holotype, A. ANSP 11228, B. ANSP 11229, and C. ANSP 11230. Scale = 10 mm.

Cope (1867b) later referred some of Wyman's (1850) specimens from Richmond, VA to this species, although he apparently had some doubts as to whether Wyman's material was closer to *S. mento* or *S. wymani*:

Squalodon mento Cope. Cetacean, Wyman, Amer.
Jour. Sci. Arts, 1850, 230-232, figs. 4, 5, 6, 7.

A tooth, perhaps occupying that place [the "transitional molar"] or the next, has been figured by Dr.

Wyman (Supra fig 4), as belonging to the genus *Phocodon* Agass. The anterior premolars and a portion of the mandible, no doubt belonging to the same species, are figured in the same place as above. They belong to an animal much smaller than that to which the teeth above described pertain, and it is a matter of some question whether these specimens do not rather relate to the *S. wymani* Leidy.

Later, Leidy (1869) referred this species to the genus *Delphinodon*, as *Delphinodon mento*. Spamer et al. (1995) indicate that ANSP 11228, 11229, and 11230 are the holotype material of *S. mento* (Figure 4), with a note that a fourth tooth is missing. Only one of these teeth (ANSP 11229- Figure 4 B) shows any similarity to the teeth of squalodonts, although the amount of enamel ornamentation, as well as the relatively short crown compared to the overall length of the tooth, are more similar to the kentriodontid *Hadrodelphis calvertense*. Dawson (1995) considered one of these teeth (apparently ANSP 11228) to be similar to, but still distinct from, *Hadrodelphis calvertense*. Until its affinities can be determined, *Delphinodon mento* should be placed in *Odontoceti incertae sedis*.

This leaves Wyman's (1850) specimens from the Calvert Formation of Richmond, Virginia (Figure 5). One tooth (Wyman, 1850: fig. 4), which he called *Phocodon*, apparently is ANSP 11227, the holotype of *Phocagenus venustus* Leidy 1869, although as noted by Leidy (1869) Wyman's figure is not very similar to the actual tooth. The other teeth figured by Wyman (1850: figs. 7a-7c) and referred to *S. mento* by Cope (1867b) have apparently been lost (Spamer et al. 1995). Based on Wyman's figure, these teeth bear no resemblance to any squalodont tooth; the teeth shown in his Figures 7a and 7b seems somewhat similar to *Phocagenus venustus*. Also figured is the anterior part of a rostrum (Wyman, 1850: figs. 5 and 6). Wyman compared it to *Phocodon*, *Delphinus*, and *Basilosaurus*, and to crocodiles, and thought that it most closely resembled *Delphinus*. In fact, his figure closely resembles the

mandible of *Squalodon calvertensis*. Unfortunately, I have been unable to locate this specimen.

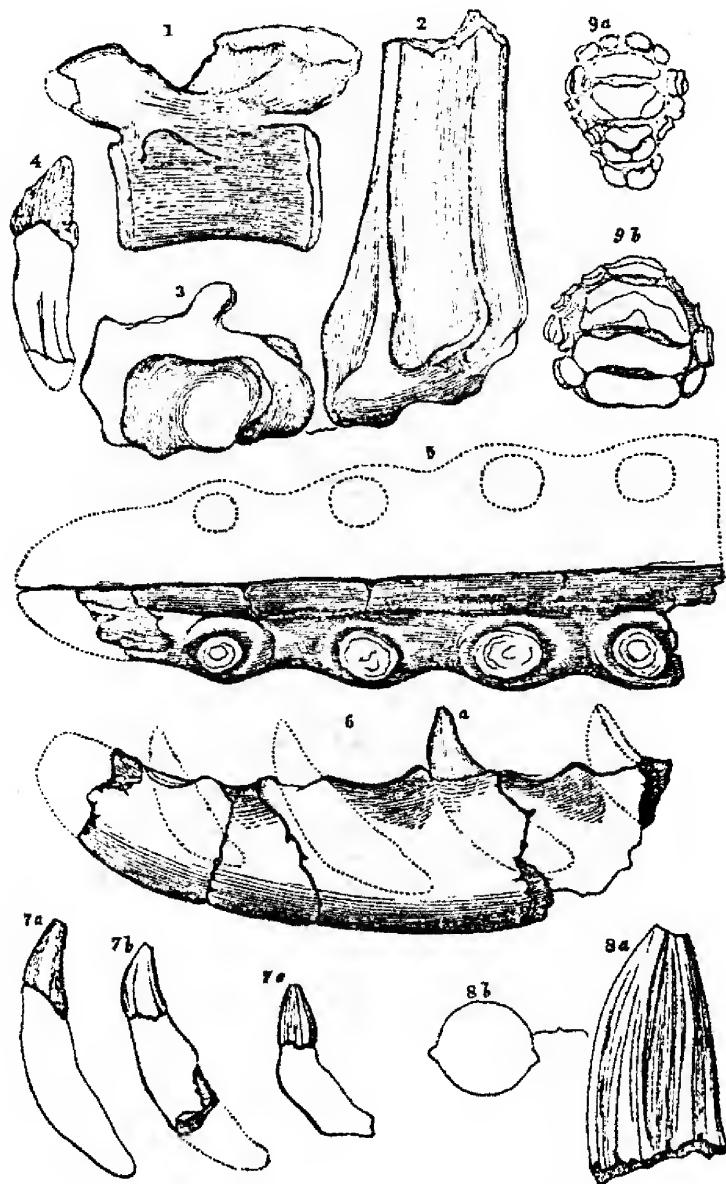


Figure 5. Wyman's (1850) figures 1-8, p.232 of American Journal of Science, V10 No. 29.

SQUALODON PROTERVUS Cope 1867b

Squalodon protervus Cope 1867b was based on a single tooth (ANSP 11543a) from Charles County, Maryland. In the same paper in which Cope named *S. protervus*, he also referred the species to *Cynorca*, creating the name *Cynorca proterva*. Cope listed two other teeth (ANSP 10326 and 10327) in the description of *S. protervus*, but the holotype was clearly the single tooth. Later, Cope (1868) assigned ANSP 11543a to the peccaries:

In the description of *Cynorca proterva*...I unfortunately mingled with its molar and premolar teeth (ANSP 10326 and 10327) the canine of [a] small *Dicotyles*. This point, suggested to me by Leidy, I have no doubt is the case.

As pointed out by Spamer et al. (1995), as the canine referred to *Dicotyles* was the holotype of *Cynorca proterva*, this forms the binomen *Dicotyles protervus*.

Leidy (1869) discussed ANSP 11543a under the name *Dicotyles lenis*. The other two teeth described by Cope (ANSP 10326 and 10327) as well as two additional teeth from South Carolina (ANSP 10328 and 10329) Leidy considered as *Squalodon protervus*. In addition, as Kellogg (1923) pointed out:

"The tooth mentioned above [*Squalodon protervus* or *Cynorca proterva* of Cope] was clearly designated as the type by Cope, and since it was originally described as a species of the genus *Squalodon*, it invalidates any subsequent use of this specific name in this genus. There are four teeth, however, labeled with this name, from Ashley River, South Carolina, in the Academy of

Natural Sciences in Philadelphia [ANSP 10326-10329].

Two of these teeth are figured by Leidy and described under the name of *Squalodon protervus*. Whatever the determination of this last mentioned material may eventually prove to be, it is evident that the use of the specific name *protervus* in this sense is invalid."

These teeth are very small, and their ornamentation pattern is different than that described in character 6 as a squalodont apomorphy. Thus, neither *S. protervus* Cope nor the teeth listed as *S. protervus* by Leidy is squalodont. As the holotype (and only the holotype) of *S. protervus* Cope has been placed among the peccaries, ANSP 10326-10329 are not currently assigned to any species.

PHOCA WYMANI Leidy, 1853a and
SQUALODON WYMANII Cope, 1867b

The history of *Phoca wymani* Leidy, 1853a was traced in detail by Ray (1976). The type specimen, consisting of cranial fragments, was collected from the Calvert Formation at Richmond, Virginia, by Wyman, and described but not named by him in 1850. Leidy (1853a) named this specimen *Phoca wymani*, and subsequently (Leidy, 1856b) reported a tooth, "apparently an inferior canine," from the Miocene of Virginia and referred it to *P. wymani* (Figure 6).

Cope (1867b) removed this tooth from *Phoca* and made it the type of a new species, *Squalodon wymani*. Cope also mentioned three other teeth supposedly belonging to this species but clearly designated Leidy's tooth (ANSP 11225) as the type:

Of this, the smallest species of the genus, three premolar teeth [ANSP 11222, 11223, and 11226] are in the collection, and the type specimen [ANSP 11225] is in the Academy's Museum. The teeth are remarkable for

the abrupt posterior direction of their crowns. The roots are curved, one of them abruptly so, and flattened.

Leidy (1869) acknowledged that these teeth were indeed cetacean but differed with Cope in his interpretation, and referred *S. wymani* to *Delphinodon*:

Three teeth, from the miocene formation of Charles County, Maryland, ascribed by Prof. Cope to a species of *Squalodon*, appear to me, at least in part, to belong to a smaller species of *Delphinodon*.

One of the teeth ... bears a resemblance to that first described of the larger species....

A tooth ... from the miocene formation of Virginia, originally ascribed by me to the same species as the remains of a Seal described by Prof. Wyman, is very like the one above indicated....The remaining two teeth from Charles County, ascribed by Prof. Cope to *Squalodon Wymani*, are different from the proceeding, and it is uncertain whether they belong to the same animal.

To further confuse matters, Hay (1902) renamed the material, stating that "... the name *Delphinodon leidyi* is intended to replace *D. wymani* Leidy ...The type of *D. leidyi* is Leidy, J.1869 A, pl. XXX, fig. 12" [ANSP 11225]. As Ray (1976) noted:

The new name must have been proposed under the erroneous belief that *Phoca wymani* and *Delphinodon wymani* were specific homonyms, which they were not and are not. In my opinion *Delphinodon leidyi* was an unnecessary replacement name and should be relegated to the junior synonymy of *Delphinodon wymani*.

Thus, *Squalodon wymani* consisted of the holotype tooth (ANSP 11225) and three referred specimens (ANSP 11222, 11223, and 11226), two of which (including the holotype) Leidy placed in *Delphinodon*. With the referral of the holotype specimen to *Delphinodon*, there is no holotype specimen of *Squalodon wymani*, and the two referred teeth that Leidy did not assign to *Delphinodon* are not currently with any genus.

The holotype tooth of *Delphinodon wymani* and the unnamed teeth originally referred to *S. wymani* are all much smaller than any known squalodontid specimen and their shape is inconsistent with any squalodontid teeth. The crowns of these teeth are recurved and nearly circular in cross section, but the only squalodont teeth that are nearly circular in cross section are the incisors, which are very large and not recurved. Thus, *Delphinodon wymani* and the unnamed specimens do not appear to be members of the Squalodontidae and should be placed in Odontoceti *incertae sedis* until their affinities can be determined.



Figure 6. *Delphinodon wymani* (Cope) 1867, ANSP 11225, holotype tooth. Scale = 10 mm.

PHOCA DEBILIS Leidy, 1856b and
SQUALODON DEBILIS Cope, 1867b

Phoca debilis Leidy, 1856b was described on the basis of three teeth from the Ashley River in South Carolina. Cope (1867b) referred this species to *Squalodon*, and later Kellogg (1923) tentatively assigned it to

Delphinodon. In Cope's (1867b) referral, however, he did not mention the type specimens, refer to Leidy's description of *Phoca debilis*, nor even mention *S. debilis* in the text, although the other five squalodonts that he listed are all discussed. I can find no reference to *S. debilis* earlier than 1867 and, because no type is designated *Squalodon debilis* does not meet the requirements of Articles 12 and 16 of the International Code of Zoological Nomenclature and the species is therefore a *nomen nudum*.

The type teeth of *Phoca debilis* formerly were ANSP 10322, 10324, and 10325. ANSP 10322 later became the type of *Phoca modesta* (see below). Gillette (1975) listed the type of *Phoca debilis* as ANSP 10324 and 10325, "3 teeth, present," but in my examination of the teeth only two were present. Neither bears any resemblance to any squalodont tooth.

PHOCA MODESTA Leidy, 1869

The history of *Phoca modesta* Leidy, 1869 is entwined with that of *Phoca debilis*. As mentioned above, Leidy (1869) designated one of the type teeth of *Phoca debilis* as the type of *Phoca modesta*, but he thought that it may have represented a squalodontid. The holotype is ANSP 10322 and, according to Gillette (1975), ANSP 10323 is a paratype (Figure 7). Allen (1880) referred this species to *Squalodon*, as *Squalodon modestus*. Kellogg (1923) was of the opinion that the teeth were from a pinniped. These teeth do not meet the characteristics described in character 6. They are much smaller than any known squalodontid tooth, and the enamel ornamentation is much less prominent and complex. Ray (1976) stated:

In my opinion both taxa [*Phoca debilis* and *Phoca modesta*] represent small porpoises, neither *Delphinodon* nor *Squalodon*, whose affinities may or may not be determinable by thorough comparison with other taxa, including modern representatives, but which in any event are not pinnipeds.

Thus, the referral of this species to *Squalodon* should be rejected, and “*Phoca*” *modesta* should be assigned to *Odontoceti? incertae sedis*.



Figure 7. *Phoca modesta* Leidy, 1869. Holotype, ANSP 10322 (left), and paratype, ANSP 10323 (right), teeth. Scale = 10 mm.

SQUALODON? PELAGIUS Leidy 1869

Squalodon? *pelagius* Leidy, 1869 was based on a fragment of the left maxilla with a cheek tooth *in situ*, from the Ashley River near Charleston, South Carolina. Kellogg (1923) stated that the holotype is in the Academy of Natural Sciences of Philadelphia, but Gillette (1975) and Spamer et.al (1995) did not list it among the Academy's collections, and I have been unable to locate it. Fordyce (1981) thought that this tooth was similar to that of *Xenorophus sloanii*. At present, this specimen is best placed in *Odontoceti incertae sedis*.

GRAPHIODON VINEARIUS Leidy, 1870

Graphiodon vinearius Leidy, 1870 was based on a tooth from Martha's Vineyard, Massachusetts (Figure 8). Cope referred it to *Squalodon* in 1890. Kellogg (1923) was of the opinion that this tooth might be from a physeterid. This specimen has a conical crown with and

inflated root, and is quite similar to other physeterid teeth. *G. vinearius* should be placed in Physeteridae? *incertae sedis*.

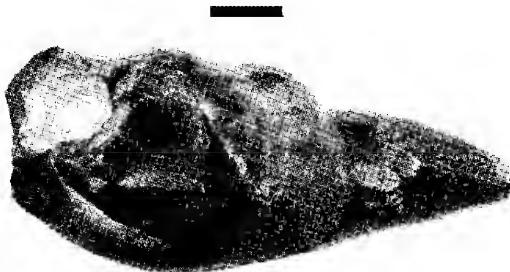


Figure 8. *Graphiodon vinearius* Leidy, 1870. Holotype, USNM 875, tooth. Scale = 10 mm.

CETERHINOPS LONGIFRONS Leidy, 1877

Ceterhinops longifrons Leidy, 1877 was based on a partial cranium (ANSP 11420; Figure 9) from South Carolina. Leidy considered this species to be close to the squalodontids. Kellogg (1923) thought that the specimen was referable to *Eurhinodelphis*; the size and overall morphology of ANSP 11420 are consistent with this assessment. Sanders (pers. comm., 2002) has noted the presence of Pliocene sediment in cavities in this specimen, although it could have been reworked from the Miocene. Given the similarity of this specimen to *Eurhinodelphis*, *C. longifrons* should be placed in Eurhinodelphidae? *incertae sedis*.

SQUALODON TIEDEMANI Allen, 1887

Squalodon tiedemani Allen, 1887 was described on the basis of a large rostral fragment found in a phosphate dredge from the Wando River at Charleston, South Carolina (AMNH 475; Figure 10). He referred two mandibular fragments from the same area to this species. Kellogg (1923) examined the holotype of *S. tiedemani* but was unable to decide whether or not this specimen was a squalodontid or an archaeocete. Incidentally, Kellogg listed this specimen as No. 10445, but



Figure 9. *Ceterhinops longifrons* Leidy, 1877. Holotype, ANSP 11420, cranium. Scale = 50 mm.

this was a field number rather than a catalog number. Boreske *et al.* (1972) referred a rostrum and mandible fragment from North Carolina to this species. Dooley (1991) described a skeleton (USNM 183023) collected in 1975 from the Calvert Formation of Virginia, and referred this and a number of skull and mandible fragments from the Calvert Formation of Maryland and Virginia and the Pungo River Formation of North Carolina to *S. tiedemani*. However, examination of undescribed specimens at the Charleston Museum in South Carolina shows that the holotype specimen of *S. tiedemani* is very similar to the anterior rostrum of the late Oligocene "Genus Y" of Whitmore and Sanders (1977), mentioned above in relation to *Saurocetus gibbesii*. It is likely that the holotypes of *Saurocetus gibbesii* and *Squalodon tiedemani* are from the same late Oligocene deposits as "Genus Y", all being found within a few miles of each other. The cranial anatomy of "Genus Y" is quite different from that of USNM 183023, so this material cannot be placed in Squalodontidae. *S. tiedemani* should therefore be placed in Odontoceti *incertae sedis*. The association of *S. tiedemani* with "Genus Y" leaves USNM 183023 and other large squalodont material from the Miocene without a name. This material represents a currently undescribed species.

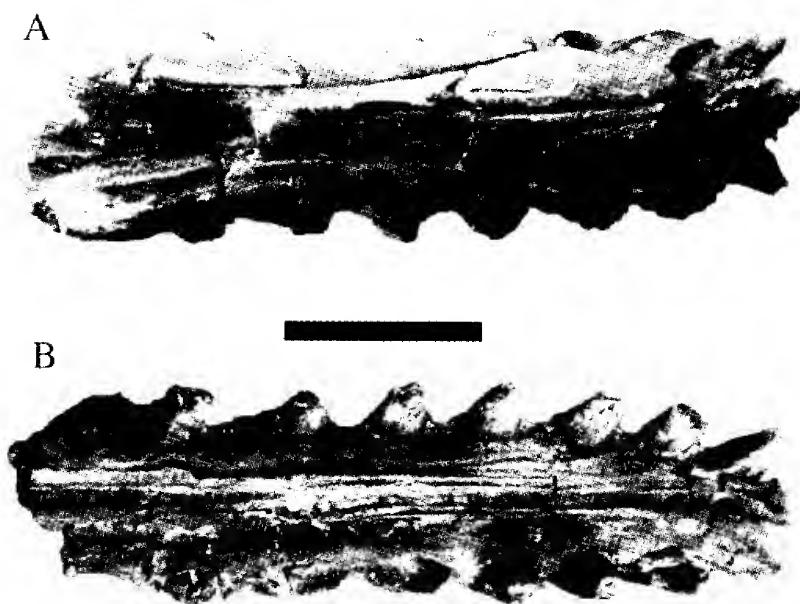


Figure 10. *Squalodon tiedemani* Allen. Holotype, AMNH 475, rostrum. A. dorsal, and B. ventral. Scale = 10 cm.

SQUALODON CALVERTENSIS Kellogg, 1923

Squalodon calvertensis Kellogg, 1923 was described on the basis of a skull, mandible, numerous teeth and five vertebrae (USNM 10484) from "Zone 6" of the Calvert Formation in Calvert County, Maryland. To date this is the best-documented squalodont from North America, and at least five other skulls and hundreds of teeth have been referred to it on collections labels. Some of the skull, mandible, and tooth remains mentioned by Kellogg (1923) (USNM 10695) are referable to *S. calvertensis*.

SQUALODON CRASSUS Allen, 1926

Squalodon crassus Allen, 1926 was based on a worn fragment of a mandible with no teeth, from the Oligocene of South Carolina (MCZ 16965; Figure 11). As Allen noted, the specimen is somewhat different

from the holotype of *S. calvertensis*, but it does have alveolae for double-rooted teeth. It is unlikely that this material is diagnostic; the morphology of this specimen is consistent not only with the Squalodontidae, but also with many other odontocetes from the Oligocene and Miocene. As it does not meet any of the listed characteristics of the Squalodontidae, *S. crassus* is placed in Odontoceti *incertae sedis*.

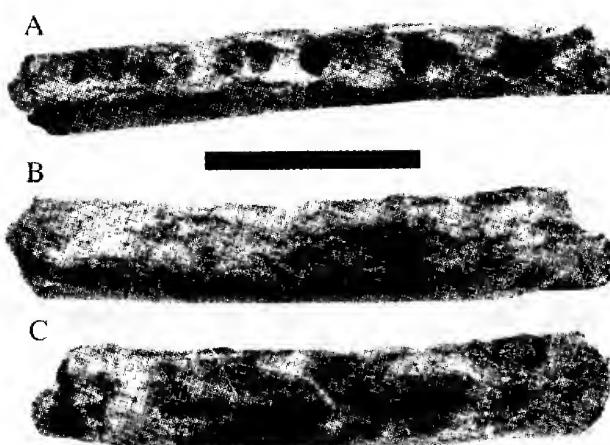


Figure 11. *Squalodon crassus*. Holotype, MCZ 16965, mandible. A. dorsal, B. medial, C. lateral. Scale = 10 cm.

SUMMARY

The present status of North American squalodontid nomenclature is as follows:

Saurocetus gibbesii Agassiz, 1848. Not a squalodontid, possibly "Genus Y" of Whitmore and Sanders (1977). Odontoceti *incertae sedis*.

Squalodon pygmaeus (Müller), 1849, Leidy, 1869 = *Agorophius pygmaeus* Müller, 1849. Not a squalodontid. Agorophiidae.

Colophonodon holmesii Leidy, 1853. Holotype lost.

Squalodon atlanticus (Leidy), 1856, Cope, 1867b. Squalodontid, but not based on species-diagnostic material. Squalodontidae *incertae sedis*.

- Squalodon mento* Cope, 1867a, = *Delphinodon mento*, Leidy, 1869. Not a squalodontid, Odontoceti *incertae sedis*.
- Squalodon protervus* Cope, 1867b, = *Cynorca proterva* (Cope), 1876b, = *Dicotyles protervus* (Cope), 1868. Not a squalodontid.
- Squalodon wymani* Cope, 1867b = *Delphinodon wymani* (Cope), 1867, Leidy, 1869. Not a squalodontid, Odontoceti *incertae sedis*.
- Squalodon debilis* Cope, 1867b. *Nomen nudum*.
- Squalodon modestus* (Leidy), 1869. Not squalodontid. "Phoca" *modesta*, Odontoceti? *incertae sedis*.
- Squalodon?* *pelagius* Leidy, 1869. Type lost? Possibly a xenorophid (Fordyce, 1981).
- Graphiodon vinearius* Leidy, 1870. Physeteridae *incertae sedis*.
- Ceterhinops longifrons* Leidy, 1877. Not a squalodontid, probably a eurhinodelphid. Eührinodelphidae? *incertae sedis*.
- Squalodon tiedemani* Allen, 1887. Not diagnostic. May be "Genus Y" of Whitmore and Sanders 1977. Odontoceti *incertae sedis*.
- Squalodon calvertensis* Kellogg, 1923. Valid.
- Squalodon crassus* Allen, 1926. Affinities not yet determined, probably not a squalodontid. Odontoceti *incertae sedis*.
- Undescribed species, "*S. tiedemani*" of Dooley, 1991.

Thus, squalodontid diversity in North America is not nearly as great as it might appear from early species lists. Only one of the 16 earlier species can be considered a valid squalodont, and it appears that there were only a small number of species, perhaps only two, living on the western Atlantic Coast.

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